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A NEW FORM OF *DIPLOCAULUS*

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To all who have worked with the genus *Diplocaulus*, the great variety in the shape of the skull and the peculiarities in other parts of the skeleton are known. Even after the analysis of the group by Case, Williston, Douthitt, and others the several species assigned to the genus are not entirely satisfactorily defined and there are many details of the anatomy still to be determined.

Recently, through the courtesy of Professor R. D. Salisbury and with the assistance of Mr. Paul C. Miller, the writer was permitted to examine the many specimens of *Diplocaulus* in Walker Museum, the University of Chicago. Among the materials is a recently discovered specimen which, because of its distinctness from described forms and the possible light it throws on the development of the Diplocaulian characteristics, is worthy of description.

Diplocaulus primigenius SP. NOV.

The material herein described consists of a large skull of the type designated by Case¹ as *D. magnicornis*, nine dorsal vertebrae, seven ribs, and a fragment that the writer takes to be a part of the right clavicle. All these parts are well preserved and have been skilfully prepared and mounted on a plaster base by Mr. Miller.

When found the vertebrae formed a curved, but unbroken series extending back from near the posterior border of the skull. At least one of the anterior vertebrae is missing. The ribs lay in an orderly pile to one side of the vertebrae.

THE SKULL

While the skull is essentially complete, its state of preservation prevents a detailed description of its characteristics. Little or

¹ E. C. Case, "Revision of the Amphibia and Pisces of the Permian of North America," *Carnegie Inst. of Washington, Publication No. 146*, (1911), p.21.

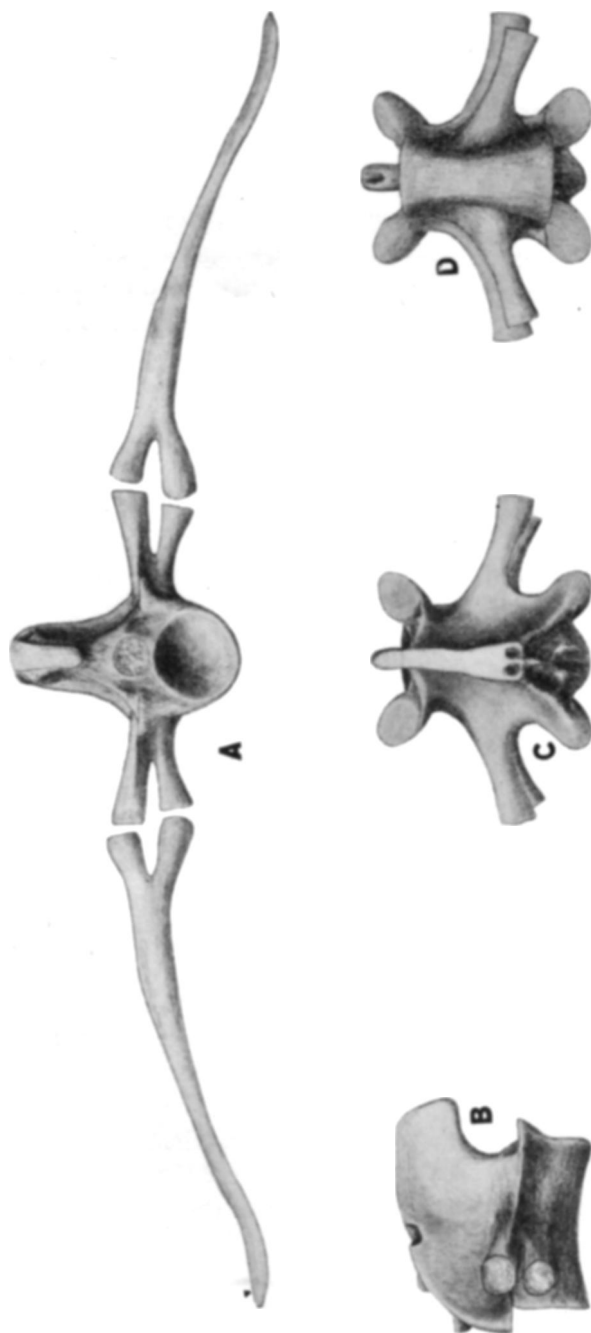


FIG. 1.—*Diplocaulus primigenius*: A, anterior view of sixth(?) vertebra with ribs attached; B, C, and D, the same vertebra from the right side, from above, and from below. All figures slightly under $\frac{2}{3}$ natural size.

nothing can be determined concerning those points bearing on the less well-established relations of the various elements. The palate surface has been crushed and lost in part and only the proximal end of the right ramus of the lower jaw is preserved.

A few sutures can be definitely determined, chiefly those of the dorsal surface back of the orbits. In these no departure from the arrangement as shown by Douthitt¹ is noted, but the doubtful portion about the orbits and nares can be neither verified nor disproved. In its general appearance there is nothing to distinguish this skull from any other of a dozen that have been referred to *D. magnicornis*. Although the posterolateral horns are broken off near the tips they are undoubtedly of the bluntly pointed, non-curved variety. The posterior border of the skull is broadly

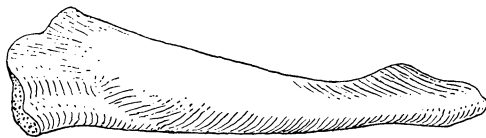


FIG. 2.—*Diplocaulus primigenius*: scapular process of right clavicle from the inner side. Natural size.

concave. None of the details such as the forward extent of the frontal and the arrangement of the vomerine teeth as stressed by Case² can be determined. The sculpture of the facial region is decidedly not radial.

The length of the skull along the median line is 116 mm. The tabular horns project back from the posterior border of the skull at the median line a distance of 78 mm. and extend 338 mm. from tip to tip.

The borders of the orbits are largely restored, but the indications are that these openings were above the average in size, possibly as much as 17 mm. or more in diameter.

The possibility of a gill chamber beneath the broad base of the posterolateral horns has been pointed out by Williston, Douthitt, and others. The notch made by the more or less abrupt ending of the

¹ Herman Douthitt, "The Structure and Relationships of *Diplocaulus*," *Contributions from Walker Museum*, Vol. II, No. 1 (1917).

² *Op. cit.*, p. 21.

quadratojugal near the mid-length of the horns on their under-side apparently forms the anterior border of an opening for the entrance of water into the gill chamber. In most *Diplocaulus* skulls there is a depressed area along the quadratojugal-squamosal union which increases in depth toward the notch, possibly to direct water into the opening. In the specimen herein described the notch is unusually pronounced and the depression leading to it is longer, deeper, and more nearly smooth than is commonly noted.

THE VERTEBRAE

The real interest in the material centers in the vertebrae, especially in their exceptionally large size and in the development of the neural spines. While there is no means of determining accurately the position of the series in the vertebral column, it is assumed that they are from the anterior end, very likely numbers 3 to 11. The first of the preserved series is somewhat shorter than any that follow and it alone has a conspicuous lateral expansion of the neural spine, a condition that suggests its proximity to the skull. Furthermore, this vertebra is the only one of the series that lacks the characteristic pit in the top of the spine, a feature more or less well developed in all the anterior vertebrae except in numbers 1 and 3 in several specimens of the described types examined by the writer.

The string of nine connected vertebrae measures about 354 mm. While this length is made up in a small part of matrix separating the centra, the figure serves well for comparison of this with previously described forms of *Diplocaulus*. The average length of a like number of vertebrae from the same region of the column in several specimens in Walker Museum is but little more than half that given above. All other dimensions of the vertebrae herein described are correspondingly large. So striking is the size that were it not for the fact that in nearly every other detail the vertebrae are those of the typical *Diplocaulus* there might be some doubt as to their identity.

In length the centra increase from about 25 mm. at the anterior end of the series to 40 mm. at the posterior end. The greatest increase is between the first and second, an increase of 5 mm.

The lower side of the centrum is markedly concave anteroposteriorly and distinctly convex from side to side at mid-length.

The diapophysis is somewhat longer than the parapophysis. Both arise from about the mid-length of the vertebrae, the former from the arch and the latter from the centrum. They are united for a short distance at their base. Both increase in diameter toward the distal end where they are distinctly enlarged.

In the described forms of *Diplocaulus* the neural spine has but little development. It is usually little more than a sharp, ridgelike thickening of the arch over the neural canal. In the vertebrae herein described one of the most conspicuous features is the spine development. For the most part the spines are comparatively high with flat, more or less rugose tops. The first of the series is distinctly expanded laterally at its top. It is only in the last two of the series that there is a suggestion of the sharp, keel-like degeneracy of the spine and even in these two vertebrae it rises distinctly above the arch. The ratio between the portion below and above the plane of the zygapophyses throughout most of the column is 4:7 while in the average previously known form the ratio is 4:4. In the last two vertebrae of the present specimen the ratio is about 4:5.

One of the characteristic features of the vertebrae of *Diplocaulus* is the presence of a pitlike depression on the top of the spine. There is a great variety in this pit development ranging from very small, round openings to rather pronounced, laterally elongate depressions. In one string of eleven connected vertebrae, No. 1016 in the Walker Museum Collections, the pits seem to be entirely lacking in all back of the fifth. The first pit is in the second vertebra in every case. Usually it is very conspicuous and more or less quadrangular in shape. The third vertebra apparently lacks the pit. In the following vertebrae the number with pits probably varies from individual to individual. For the most part there is no suggestion of an anteroposterior constriction or division of the pit into two distinct facets and in no specimen except the one herein described has the writer seen distinctly double pitting. In the present specimen, however, in each vertebra except the first of the preserved series which is pitless, the spine depressions are

distinctly paired. In most cases the depressions are connected by a very shallow and narrow groove, but in one or two of the vertebrae the openings are distinct. The size of the pits is another distinctive feature of this form. Between the lateral margins of the pits of the fourth vertebra is a distance of 7 mm. and in every case the pits are so large and so widely separated that the spine is distinctly swollen for their accommodation. Clearly, whatever the function of these pits it was more fully exercised in this than in any of the other forms that have been observed.

As in the typical *Diplocaulus*, the articular faces of the zygophyses are directed straight up and down so that their common plane furnishes a plane of reference for describing proportions. The zygosphenes and zygantrum is strongly developed throughout the series of vertebrae. Posteriorly the neural spine divides to send strong buttresses down, out, and back to the posterior zygophysis. Between these buttresses there extends back in a horizontal plane a spoutlike projection, the zygantrum. The spine of the preceding vertebra extends forward as a vertical plate running in the groove or spoutlike zygantrum without any noticeable modification for the articulation. There is a suggestion of further strengthening of the intervertebral articulation through a more or less pronounced vertical keel between the posterior, zygopophysial lamellae at the anterior end of the zygantrum excavation. Some of the vertebrae show a corresponding excavation on the lower anterior edge of the zygosphenes extension of the spine.

The following table comparing the various dimensions of the present specimen with those of the common type, No. 1018 in the Walker Museum Collections, will serve to emphasize the differences.

	W.M. No. 564	W.M. No. 1018
	mm.	mm.
Length of centrum.....	40	22
Dist. across transverse processes....	70	44
Greatest height.....	40	23
Below plane of zygo.....	14	12
Above plane of zygo.....	26	11
Across zygopophysies.....	36	21

THE RIBS

Of the ribs preserved none resembles the comparatively short, straight, distally expanded form figured by Douthitt¹ in the neck region of his skeletal restoration, and commonly found in the large collections of *Diplocaulus* material. It is entirely possible that none of the typical anterior ribs were preserved. Those present were in a more or less connected pile and not directly articulated with the vertebrae. It is assumed, however, that they belong near the anterior end of the preserved string of vertebrae where they were found, and represent a more primitive stage in the development of *Diplocaulus*. Their exceptional curvature and length are at once striking. Only one is preserved in its entire length. This measures 111 mm. Some of the other ribs were evidently shorter than this but for the most part they indicate an equal or even greater length.

In the one complete rib there is a departure from a straight line of 20 mm., perhaps the average. Some are more sharply curved and others less. The distal half is essentially straight, the curvature being a gradual bending of the proximal half. The curvature is within a plane that departs little from the horizontal so that a body cross-section shows but a slight down-bending of the ribs, a condition entirely in keeping with the generally accepted conception of a broad, flat, bottom-living type. The capitulum and tubercle are both markedly expanded and undoubtedly formed a firm attachment of rib to vertebrae.

HABITS AND RELATIONSHIPS

The aquatic adaptations of *Diplocaulus* have been repeatedly pointed out by various writers. In typical forms there is much evidence that these amphibians were of the groveling, bottom-living type. So bizarre are the skull modifications and body form and so obscure are the stages leading up to this condition that any suggestions are of exceptional interest.

In several respects the form herein described seems to represent an antecedent step in *Diplocaulus* evolution. At least it offers some pointed suggestions as to the several stages through which

¹ *Op. cit.*

the group passed. The large, strong vertebrae; the well-developed spines, and the highly curved ribs approach the normal condition of the more generalized Stegoceph. The well-developed zygosphenes and zygantrum articulations bespeak a strength and flexibility of the vertebra column such as belongs to a creature that has developed swift progression through the water by means of tail propulsion.

The remarkable pit development on the spines of this form suggests a still further step in its modifications for swift movement through the water. It seems highly probable that the pits formed an articulation for anteroposteriorly movable spines that gave support to a dorso-median fin. The lateral rigidity of such a fin was assured by the double articulation indicated by the well-developed double pits. As would be expected, the anterior fin spine gives evidence of its superior size and strength of articulation through the very conspicuously larger pit on the second spine. The present specimen lacks the first vertebra, but the several strings of previously known forms examined by the writer establish this point. In the backward folding of the fin spines extra space would be required behind the enlarged anterior spine. Perhaps this accounts for the uniform absence of the pit or pits in the third vertebra.

Not entirely in keeping with these swift-swimming modifications is the remarkable development of the shoulder girdle. The fragment that the writer identifies as the ascending process of the right clavicle is stout and something over 60 mm. long. It is strongly grooved on the outer-posterior side for articulation with the scapula. In all figured specimens of *Diplocaulus* and the many other specimens examined by the writer this process is short. In some cases it may have been broken off but after making due allowances for this it does not seem likely that there was an actual articulation with the scapula or at best, but a weak one. Perhaps the ancestral *Diplocaulus* was a creature that had become well adapted to swift progression through the water to the extent of a suitable vertebral evolution and the reduction of the limbs. At a later stage this actively swimming form likely degenerated to the groveling type in which habitat the girdles continued to reduce

in size and strength of attachment and the vertebral column lost much of its vertical rigidity through the reduction of the spines. Naturally the supports for the dorso-median fin degenerated to a smaller size and a single articular facet. Very likely in the process of flattening the body, one of the first steps was the backward twisting of the curved ribs, a stage preserved in the present specimen, and a later tendency toward straight ribs.

Of the distinctness of this form there can be no question. True, the skull differs very little from many described forms. Greater variations are undoubtedly rightly included in a single species. One might logically expect that the remarkable modifications should reach the skull and limbs before the vertebral column. While all indications are that the skull and associated vertebrae are of the same individual there is, nevertheless, a possibility that the association is of two widely differing species. For this reason the vertebrae and long, curved ribs are considered typical of the new form which the writer wishes to designate as *Diplocaulus primigenius*.

The material on which this form is based is No. 564 of the Walker Museum Vertebrate Collections in the University of Chicago. It was found by Mr. P. C. Miller in Baylor County, Texas, on Brush Creek near Seymour.

The writer takes this opportunity to express his appreciation of the kindness of Professor Salisbury in permitting the study of this material and for the courtesies shown by Mr. P. C. Miller, whose skill and painstaking care in preparing the bones have made it available.